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INTRODUCTION

This report adds to the growing published literature on coprophagy in wild chimpanzees. We present observational and circumstantial evidence of this behavioural pattern, and test the utility of current hypotheses for explaining coprophagy in wild chimpanzees.

Eating one's own feces (autocoprophagy) and eating the feces of others (allocoprophagy) occurs in wild populations throughout the animal kingdom¹. Yet in apes, coprophagy is commonly considered to be abnormal behaviour in captive populations. It often appears in lists of problematic behaviours^{2,3}, and is thought to be a response to boredom or stress⁴.

Yet wild chimpanzee populations also engage in coprophagy: Autocoprophagy has now been reported from several long term study groups, including Assirik⁵, Gombe⁶, Mahale⁷, Bossou⁸, and Fongoli (Bertolani *et al.*, unpublished data). Interspecific allocoprophagy has been reported from Kibale, where chimpanzees consume elephant dung⁹. The cause of this pattern remains uncertain, but several hypotheses have been proposed.

- (a) Boredom: Commonly cited as a factor inducing coprophagy in captivity⁴, it has also been suggested to explain wild gorilla coprophagy during long periods of heavy rain when foraging activities are reduced¹⁰.
- (b) Insufficient roughage: Lack of "wadging" materials (such as fibrous leaves) in the diet of captive chimpanzees may increase the frequency of coprophagy¹¹.
- (c) Provision of essential nutrients: Some captive groups of largely herbivorous gorillas may engage in coprophagy in order to gain Vitamin B12 which is present only in animal matter¹².
- (d) Food scarcity: At Gombe, coprophagy occurred during a period of fruit scarcity, after an unusually dry season⁶. The pressures of foraging in a food-scarce environment may increase coprophagy.
- (e) Reingesting hard seeds: Coprophagy may be adaptive when groups feed on fruits with seeds that pass through the gut whole, but then can be split open and reingested after coprophagy. Free-ranging chimpanzees in the Republic of Congo regularly engaged in coprophagy when feeding on *Dialium*

<NOTE>

Coprophagy by the semi-habituated chimpanzees of Semliki, Uganda

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seeds, which were found both whole and fragmented in feces¹³. Chimpanzees at Assirik extract and eat baobab (*Adansonia digitata*) seeds from their feces⁵. Allocoprophagy in Kibale is positively correlated with the presence of hard seeds in the elephant dung⁹. In Mahale, an individual showed coprophagy after eating *Saba florida*⁷, a species with hard seeds that are ingested whole.

- (f) Culture: Nash *et al.*³ presented evidence suggesting that coprophagy may be a socially learned behaviour in captive chimpanzee groups.

METHODS

The Toro-Semliki Reserve is in western Uganda, near the eastern edge of the Great Rift Valley (0°50' to 1°05' N, 30°20' to 30°35'E), and supports several chimpanzee communities¹⁴. Habituation efforts have been ongoing since 1996¹⁵, and progress is being made.

We made observations and collected fecal samples opportunistically from May–November 2008. Feces were washed and sieved through a 1 mm mesh, and the contents recorded.

RESULTS

We saw five episodes of autocoprophagy during the study period (See details in Table 1). No allocoprophagy was observed directly, but circumstantial evidence of coprophagy comes from one case of discarded (presumably spat-out) seeds (Table 1), and from seed fragments in eight fecal samples (Table 2).

At least three individuals, including adult and juvenile males, showed coprophagy (Table 1). Individuals were observed to defecate directly into their own hand and raise the feces to their mouth. They then manipulated the feces in their mouths using their lips, spitting out seeds and indeterminate fecal matter. These cases occurred when groups ate low-quality food items, such as bark, pith and seeds (Table 1). Case 6 occurred when at least one individual was in poor health, as evidenced by vomit found on leaves, although no evidence of disease or infection was found at any other time during the study.

The presence of seed fragments in feces may be indirect evidence of coprophagy, because the apes were never seen or heard to crush the hard *Saba florida* seeds when eating the fruits whole. In every case in which coprophagy was observed, we could hear the sounds of

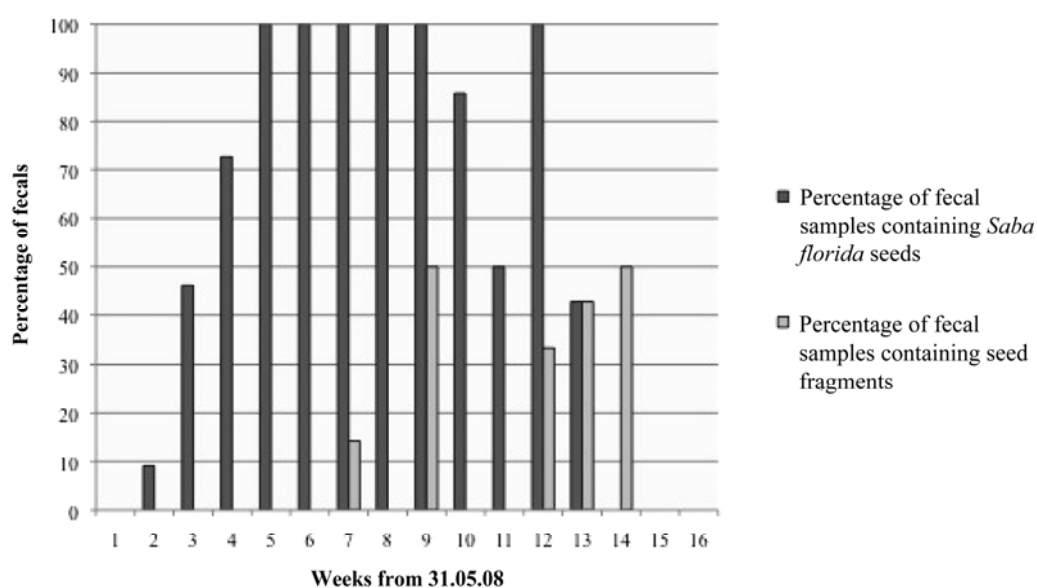
Table 1. Observed cases of coprophagy by Semliki chimpanzees.

Case No.	Date	Min. group size	Other food items	Individual	Duration of coprophagy (min)	Duration of observation (min)	Other notes
1	21.07.08	2	<i>Cynometra alexandri</i> bark/cambium	Juvenile male	32	75	Same individual as Case 4.
2	08.08.08	6	<i>Phoenix reclinata</i> pith, <i>Cynometra</i> leaves	Adult male	8	78	
3	14.08.08	25	<i>Cynometra alexandri</i> pods, <i>Cola gigantea</i> bark/cambium	Unknown	Unknown	186	Circumstantial evidence: two moist seeds (sp. <i>indet.</i>) smelling of feces fell to the ground below one individual*
4	21.08.08	2	<i>Cynometra</i> pods, <i>Acacia</i> bark/cambium	Juvenile male	11	22	Same individual as Case 1.
5	05.09.08	9	<i>Cola gigantea</i> bark	Adult male	1	141	
6	06.09.08	20	<i>Phoenix reclinata</i> pith, <i>Cola gigantea</i> bark/cambium	Juvenile male	30	103	Vomit found on leaves below group

* Case for coprophagy is strengthened by the fact that not only were the chimpanzees not seen to eat these seeds that morning, but also had spent the observation period (from un-nesting) in gallery forest, where this species was not commonly found.

Table 2. Chimpanzee fecal samples containing *Saba florida* seed fragments.

Fecal No.	Date	Other identified food items found
60	10.07.08	6 <i>Beilschmiedia ugandensis</i> seeds, 2 <i>Rhus natalensis</i> seeds, 33 <i>Saba florida</i> seeds, fiber “few”
75	22.07.08	3 <i>Saba florida</i> seeds, 3 <i>Hymenoptera</i> larvae, fiber “common”
87	11.08.08	Weaver ants, fiber “few”, <i>Ficus</i> sp. “abundant”, <i>Cynometra alexandri</i> “common”
96	23.08.08	green leaf “few”
99	25.08.08	<i>Cynometra alexandri</i> “few”, <i>Ficus mucosa</i> “abundant”, fiber “few”, green leaf “few”
101	28.08.08	Weaver ants “few”, fiber “abundant”, fruit skin “few”
102	30.08.08	Fiber “abundant”, fruit skin “common”
103	30.08.08	Weaver ants “few”

**Fig. 1.** Indirect evidence of coprophagy from fecal analysis: *S. florida* consumption.

seeds being crunched and cracked. We presumed these to be *Saba*, since these seeds were predominant and were found more consistently in fecal samples than any other seeds during the study period. We found crushed seeds in samples in the latter half of the *Saba* fruiting season (Fig. 1), shortly before *Saba* seeds disappeared from feces altogether.

The decline in the presence of whole seeds and increase in the presence of fragments in feces between Weeks 1–8 and Weeks 9–16 (Fig. 1) differs significantly from chance ($X^2_{(df=1)} = 10.7$, $N=78$, $p<0.01$).

DISCUSSION

The hypotheses (a)–(b) cannot explain coprophagy by the Semliki chimpanzees. (a): Unlike barren captive

environments, the habitat at Semliki reserve is rich and stimulating; the chimpanzees engage in various kinds of extractive foraging. (b): Fibrous materials often feature in the diet of the Semliki chimpanzees¹⁴, and were consumed during every case of observed coprophagy. (c): Insects occurred regularly in fecal samples at Semliki during the study period, so coprophagy need not supply Vitamin B12.

Instead, hypotheses (d) and (e) seem likely variables which may interact to cause the chimpanzees of Semliki to engage in coprophagy. Given the significant relationship between the presence of crushed seeds in feces and declining *Saba* availability, we propose a tentative hypothesis that coprophagy in Semliki chimpanzees is caused by the pressure to exploit added

nutrients from reingesting *Saba* seeds when availability of the fruit is in decline. There is a possibility that seed fragments in feces may not reflect coprophagy but instead the occasional crunching of the seeds during *Saba* fruit consumption that is never seen at Semliki, but observed at Mahale (Nakamura, personal communication). Further observational data are needed to clarify this.

The lack of coprophagy during times when *Saba* was consumed in abundance, and the presence of many whole, non-reingested seeds in feces in the early half of the fruiting season, suggests that coprophagy may be a fallback or seasonal strategy for Semliki chimpanzees. It may be a response to a decreasing resource, as a way of more efficiently exploiting the nutrients available from this high quality food item. It may also be specific to individuals who find it harder to acquire high quality foods (Table 1). However, further behavioural data is needed to test this, particularly since coprophagy was only observed in adult and juvenile males and these individuals are better habituated to human observation than female chimpanzees at Semliki.

Hypothesis (f) cannot be assessed from the data gathered thus far. As habituation efforts progress, it is hoped that more information on unusual behavioural patterns in this population will come to light.

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